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Larval Carnivory and Myrmecoxeny, and Imaginal Myrmecophily in Miletine Lycaenids (Lepidoptera, Lycaenidae) on the Malay Peninsula

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Abstract The life-histories of different South East Asian Miletinae (Lycaenidae) of the genera *Logania*, *Miletus*, and *Allotinus* are described. Larval sternorrhyncho-phagy is likely the plesiomorphic condition in this subfamily ; it still occurs in *Logania malayica*, where the caterpillars feed on ant-attended aphids. The imagines feed on honeydew of the same species of aphids and at night rest within the ant-attended aphid colonies. In the species-rich genera *Miletus* and *Allotinus*, different food specializations are found : *Miletus biggsii* feeds on several species of aphids as well as coccids. In all observed cases its prey was attended by ants of the genus *Dolichoderus* (Dolichoderinae), which seem to be the oviposition cue for the females. In *Allotinus apries* the L₁ caterpillar feeds on coccids, whereas the L₂ larva is carried by ants of the myrmicine species *Myrmecaria lutea* into their nests and supposedly feeds as a kleptoparasite on the ant's brood. In *Allotinus subviolaceus* the larvae feed on membracids (Auchenorrhyncha).

Introduction

Among lycaenid butterflies (Lycaenidae) the subfamily Miletinae (sensu ELIOT, 1973) is remarkable for its nutritional biology. All known miletine larvae are carnivorous (CORBET & PENDLEBURY, 1978 ; COTTRELL, 1984 ; ELIOT, 1986) and feed upon different species of homopterans, mostly Sternorrhyncha (aphids and coccids) ; sometimes they also feed on the honeydew of their prey. The adults seem to depend totally on homopteran honeydew for their nutrition. The biology of the Asian genus *Logania* DISTANT, 1884, and, especially, of the species-rich genera *Miletus* HÜBNER, 1819, and *Allotinus* C. & R. FELDER, [1865], is only poorly known (for review : COTTRELL, 1984).

In recent years, we investigated the life-histories of several West-Malaysian lycaenids, including phytophagous myrmecophilous species (MASCHWITZ *et al.*, 1984, 1985a, 1985 b). Our recent studies on the Miletini not only confirmed the carnivorous behaviour of their larvae, but also revealed some additional previously unknown aspects of their feeding habits, including, for example, a shift to kleptoparasitism (as defined below) inside ants' nests. The adaptations of the adult butterflies to the ants are in some cases closer than previously expected.

Methods

The observations for the current study were carried out in 1986 and 1987 (January to March) near the Ulu Gombak Field Studies Centre (UGFSC) of the University of Malaya, Kuala Lumpur. Observations and tests were carried out partly in the field and partly in the UGFSC. The butterflies were kindly determined by Lt. Col. J. ELIOT, Taunton, U. K. Voucher specimens of the butterflies and the membracids are deposited at the British Museum (Natural History), London. The scanning electron microphotograph was taken with a Hitachi S 500 by M. RUPPEL, Frankfurt.

Results

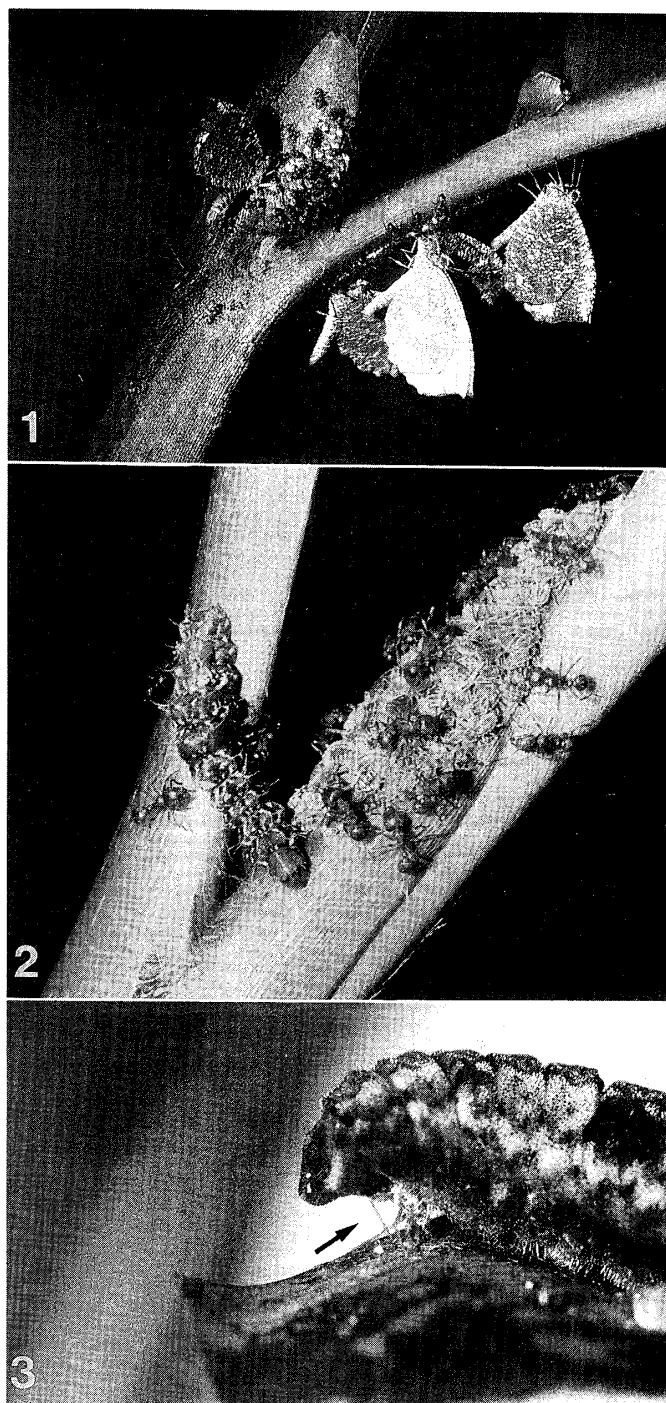
1. *Logania malayica malayica* DISTANT, 1884

Adults of this species were found in an open, disturbed part of the forest where they were feeding on the honeydew of two colonies of an aphid (*Pseudoregma* sp., Hormaphididae) on *Achasma* (Zingiberaceae). The aphids were attended by *Leptothorax* ants (Formicidae, Myrmicinae). *Pseudoregma*, like many members of the Hormaphididae, possesses a soldier caste. While one aphid colony was small and contained only a few soldiers, the other colony was very large and counted hundreds of aphids with a considerable number of soldiers. At any time, a varying number of male and female *L. malayica* was observed either "milking" the aphids with their proboscis or resting inmidst the larger colony, especially in the lower parts of the plant where there were fewer soldiers. Also at night the adult lycaenids rested within the colony (Fig. 1). Over a period of 4 weeks, between 4 and 6 butterflies were observed more or less permanently within the aphid colony.

We failed to detect any eggs or larvae of the lycaenids in the large aphid colony. As reported by OHARA (after AOKI, 1987), eggs or larvae of predators are usually destroyed by the hormaphids' soldiers. We brought caterpillars of *Miletus* spp. of different sizes (L₂ to mature) into this colony (collected from colonies of other, non-hormaphidian aphids) to test the reaction of the soldiers; the larvae were attacked at once with the cephal spines and usually fell to the ground. In a few cases younger larvae were killed by the soldiers. Only in the smaller colony with fewer soldiers we found several ova, a yellowish-brown empty chorion, and, on one occasion, a 9 mm long larva similar in habitus to the larvae of *Miletus* and *Allotinus* known to us, but much more yellowish to yellowish-olive than any of these, with an interrupted dark bluish-grey dorsal line and whitish speckling (see Fig. 2). Unfortunately the larva died in the laboratory.

2. *Miletus biggsii* (DISTANT, 1884)

Supplementary to MASCHWITZ *et al.* (1985a), additional observations on *Miletus biggsii* are reported here. In 1984 we observed females of *M. biggsii* ovipositing into colonies of coccids visited by *Dolichoderus* ants (Dolichoderinae). During an excursion



Figs. 1-3. 1. Imagines of *Logania malayica*, resting at night within an ant-attended colony of *Pseudoregma* hormaphids on *Achasma*. 2. Miletine caterpillar in *Pseudo-regma* colony attended by *Leptothorax* ants on *Achasma*; supposedly larva of *Logania malayica*. 3. Mature larva of *Miletus biggsii* while devouring an aphid (arrow). The aphid is grasped with the thoracic legs; the caterpillar's head is strongly bent ventrally under the "hood" of the prothoracic shield during the feeding act.

to Singapore in February 1986 we observed several females of *M. biggsii* flying around bamboo in the garden of the University of Singapore and ovipositing into aggregations of aphids (an unidentified hormaphid species), attended by a *Dolichoderus* sp. as well. Both the oviposition act and ova were seen, but no caterpillars. The absence of caterpillars probably again can be attributed to the presence of the hormaphid soldiers, which kill predators or throw them to the ground (AOKI, 1982, 1987).

In 1987 we observed *M. biggsii* females flying around aphid colonies of *Pseudoregma* sp. (Hormaphididae) attended by *Dolichoderus* ants on zingiberacean plants near the UGFSC and feeding on the honeydew. We found ova of *M. biggsii* both in larger and smaller colonies of the hormaphids, but larvae only in the smaller colonies which contained no or only a few soldiers. The larvae of *M. biggsii* fed upon these colonies, consuming large numbers of aphids and thus destroying the small aggregations. The feeding act of a *Miletus* caterpillar was repeatedly observed: the larva first moves its head over and around one aphid several times, then grasps it with its mandibles, draws it up and off the plant, takes it with its thoracic legs, and then devours it within a few seconds (Fig. 3). This act is repeated up to ten successive times, after which the caterpillar rests for one to several hours. When we offered different species of aphids to the caterpillars, they preferred the *Pseudoregma* species they were used to and, reluctantly, accepted also another hormaphid species from bamboo, but they rejected the non-hormaphid species offered to them.

3. Genus *Allotinus* C. & R. FELDER, [1865]

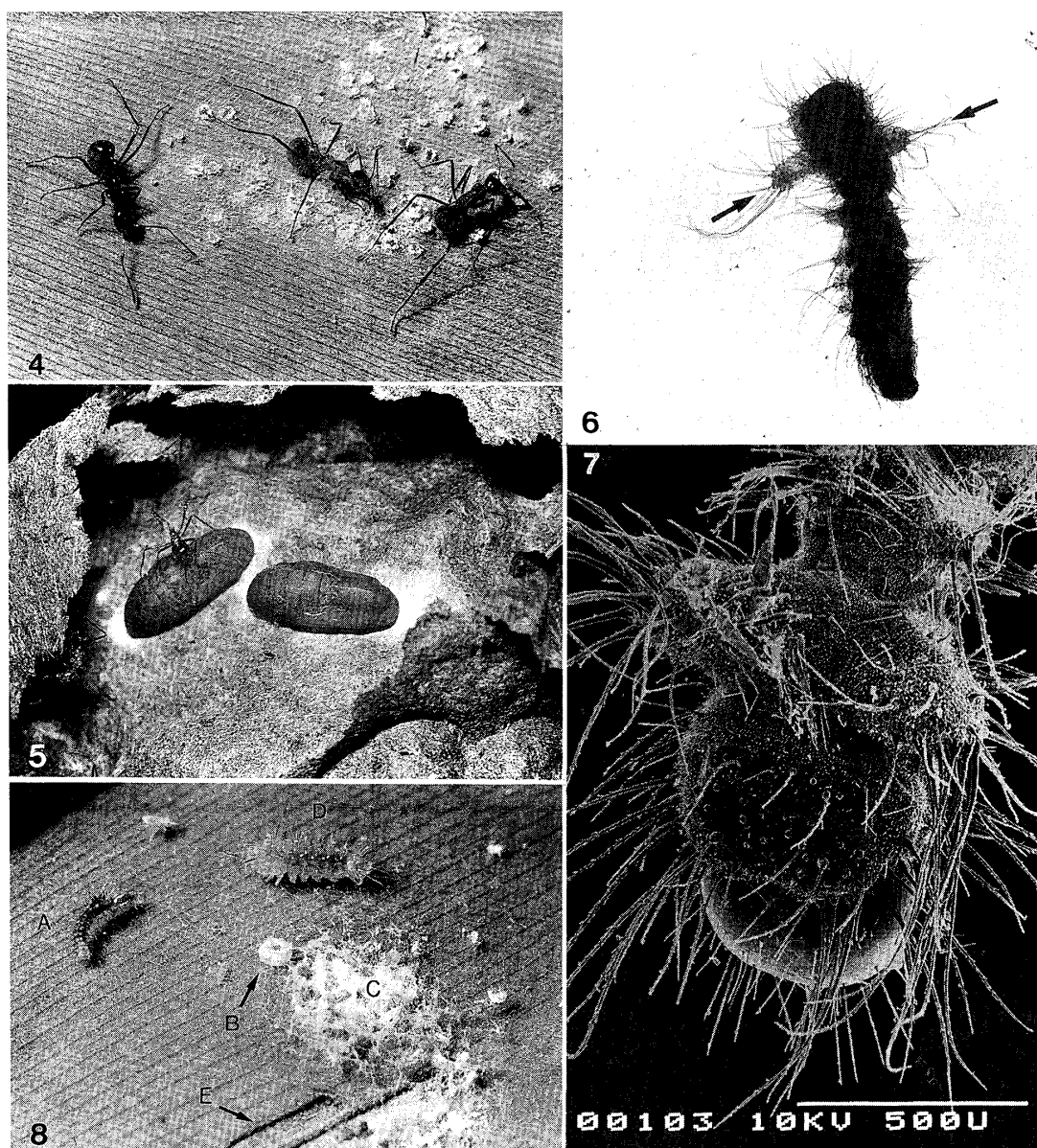
3. a. *Allotinus* (*Paragerydus*) *substrigosus substrigosus* (MOORE, 1884)

A male of *A. substrigosus* for several days stayed with a colony of *Pseudoregma* sp. (Hormaphididae) on *Achasma* sp. (Zingiberaceae) in a dense secondary forest, attended by a *Crematogaster* species (a myrmicine ant). It rested near or in the colony and fed on the honeydew excreted by the aphids in response to being "milked" by the butterfly's proboscis. The small aphid colony contained only a few soldiers. We detected eggs and a typical *Allotinus* larva within the colony. The caterpillar disappeared after a few days.

3. b. *Allotinus* (*Paragerydus*) *apries* FRUHSTORFER, 1913

During earlier stays in West Malaysia we found a few reddish brown lycaenid pupae within the carton nests of the ant *Myrmicaria lutea* EMERY, 1901 (Myrmicinae) (Figs. 4, 5). While studying this ant species in more detail in 1986 we found a total of 3 pupae, two of them while opening a carton nest on February 7th (Fig. 5). From these a female emerged on February 16th before sunrise and a male on the early afternoon of Feb. 23rd. This shows that the pupal instar may last more than 16 days, the longest pupal duration of a miletine lycaenid we observed so far under tropical conditions. From a third pupa collected on March 21st, a male emerged on April 5th.

The pupae and ten remnants of pupation sites (silken bolsters to which the pupal cremasters had been attached) were found within the nests of a *Myrmicaria* colony living on plants in a small swampy area. There, many of the carton nests of the ants



Figs.4–8. *Allotinus apries* and *Myrmicaria lutea*. 4. Workers of *Myrmicaria* attending a small aggregation of coccids on a zingiber leaf. 5. Nest of *Myrmicaria*, outer envelope removed; the two pupae of *A. apries* and their silken pupation sites are clearly visible. 6. Ventral view of 2nd instar caterpillar of *A. apries* showing the lateral protrusions on the mesothorax (arrows). 7. SEM photograph of 2nd instar larva, dorsal view of head and thorax. 8. A: first instar caterpillar of *A. apries*, hatched out of the egg B; C is the coccid colony where the larva preyed upon, nearly no coccids are left of it; D is an unidentified phytophagous first instar lepidopteran larva (lymantriid?), responsible for the excavations in the zingiber leaf; E: this caterpillar was as well not attacked by *Myrmicaria*.

had been built under leaves of bananas, zingibers, and other plants. Only large nests were occupied by lycaenids. In four other colonies of *Myrmicaria lutea* living along the

Gombak River, no pupa or pupation site was found.

The silken bolsters, to which the pupae had fixed their cremasters, were mostly located on the outer surface of the first carton layer (rarely on the second) under the outer envelope of the nest. Thus there was only a single wall (rarely two) between the pupa and the open air.

While observing freshly opened nests of *Myrmicaria* (which never contained living homopterans, but only brood, queens, and workers of the ants), we once noticed a worker ant carrying a small lycaenid larva in the same manner as ant brood between its legs and parallel to its body. The caterpillar was held by ant at lateral protrusions of its mesothorax, which are quite unusual for lycaenid larvae (Figs. 6, 7). It was accidentally killed during collecting.

Most of the homopterans visited by the *Myrmicaria* workers were scale insects. The species visited most often was a coccid that covered its feeding sites with small amounts of waxy "wool". Within such an aggregation of coccids we found an empty ovum and a 1st instar miletine caterpillar preying on the coccids (Fig. 8), but completely ignored by the ants. We took the caterpillar into the laboratory and fed it with live coccids. After the first moult, shape (including the lateral mesothoracic protrusions) and colouration were identical to the caterpillar found in the *Myrmicaria* nest. The L₂ larva did no longer feed on the remaining coccids and starved to death within less than 8 hours. This might indicate that coccids are inadequate food for L₂ larvae. Feeding tests with *Myrmicaria* brood could not be conducted. When the freshly dead caterpillar was offered to the worker ants together with *Myrmicaria* larvae of the same size, the ants showed no aggression and carried and deposited the caterpillar in the same manner as their own brood (if anything, preferring it over their own brood), and they palpated the caterpillar intensively just like their own larvae.

Though we were not able to prove it, we nevertheless are sure that the young instar caterpillars were larvae of *Allotinus apries*. In fact, these were the only lycaenids we found associated with *Myrmicaria lutea*. We checked dozens of coccid aggregations attended by dolichoderine ants without finding any *Allotinus* preimaginals. Furthermore, we frequently checked carton nests of other myrmicine ant species like *Crematogaster* spp., and of Dolichoderinae, and silken nests of *Oecophylla* sp. and *Polyrhachis* spp. (Formicinae), but never found any *Allotinus apries* pupae. Our observations on *Allotinus apries* suggest the following life-history: The female oviposits close to or into coccid aggregations attended by workers of *Myrmicaria lutea*. The 1st instar caterpillar is ignored by the workers and feeds on the coccids. The peculiar 2nd instar larva is as attractive for the ants as their own brood and is carried into their nest. There it has to feed on food other than coccids, presumably the ants' brood, within a few hours. Development of the larva seems to be quite fast, judging from the fact that we did not observe any older caterpillars during nest controls. Pupation takes place within the *Myrmicaria* nests; after a comparatively long pupal stage the imago emerges and escapes from the nest.

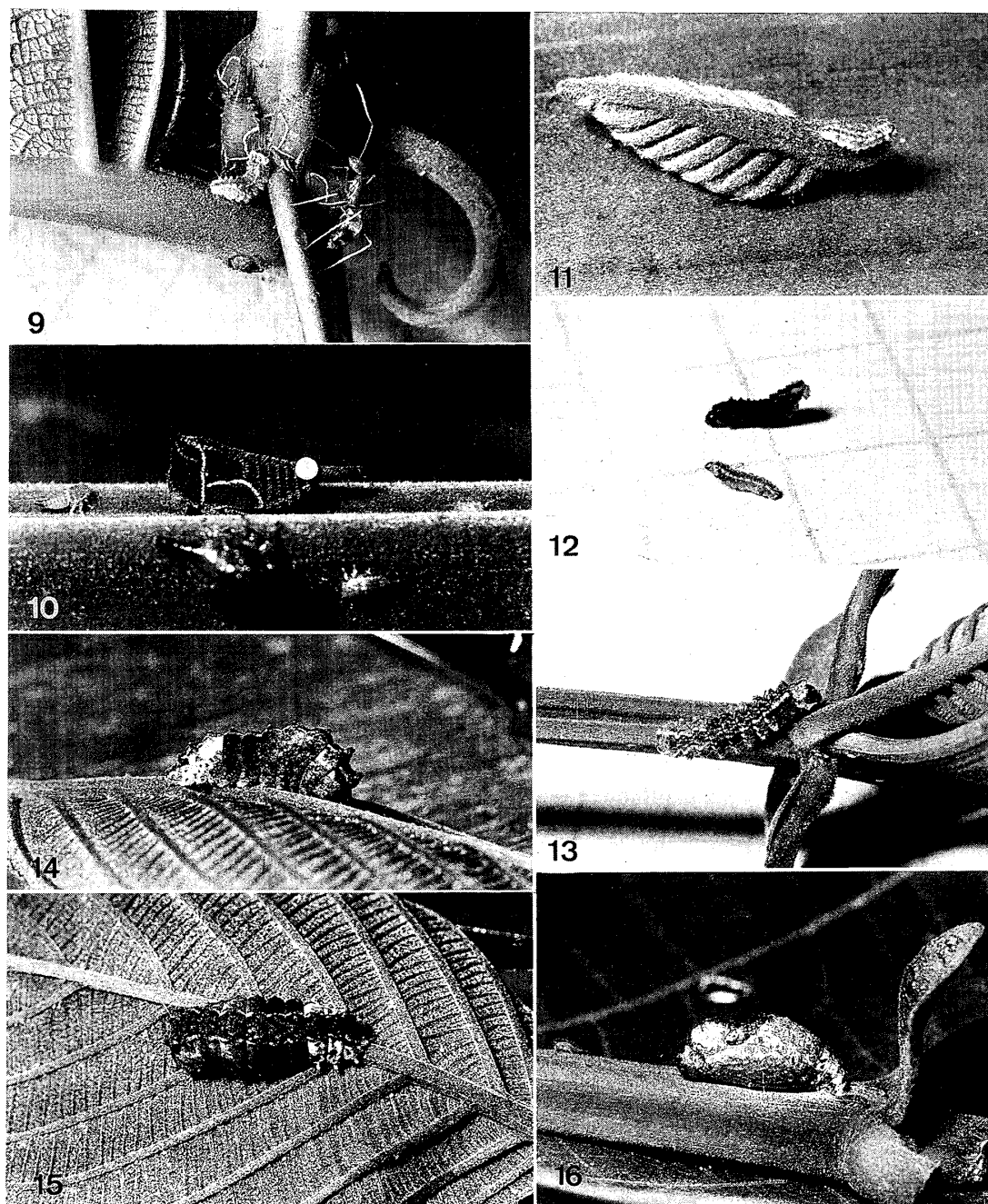
3. c. *Allotinus* (*Allotinus*) *subviolaceus* C. & R. FELDER, [1865]

Caterpillars of this species were found in a cleared area on a creeping *Uncaria* sp. (Rubiaceae) in aggregations of an unidentified species of membracids. The membracid aggregations were attended by the formicine ant *Anoplolepis longipes* (JERDON, 1851) (Fig. 9). We found lycaenid eggs and different instars of lycaenid caterpillars. The eggs were found on the *Uncaria* stems close to or in the homopteran aggregations and, on three occasions, directly on older nymphs (Fig. 10). The caterpillars were observed to prey exclusively on young membracid larvae. Ectoparasitic behaviour as described by KITCHING (1987) in *Allotinus* (*Allotinus*) *major* C. & R. FELDER, [1865], could not be observed. L₂ and older caterpillars were observed grasping 1st and 2nd instar membracids with their thoracic legs and feeding on them.

The rearing of the caterpillars turned out to be difficult under laboratory conditions. The membracids left the cut twigs so that the younger caterpillars starved to death. One older caterpillar fed on a freshly killed nymph, but younger larvae did not accept dead food. Only one of our larvae pupated on the stem of the plant, producing a male butterfly.

The chorion of the ovum of *A. subviolaceus* is white (Fig. 10). The first instar caterpillar (Figs. 11, 12) is reddish dorsally (similar to the hairy covering of the young tips of *Uncaria* shoots) and slightly yellowish brown ventrally. Head and prothoracic shield are blackish. The subdorsal rows of warts are whitish, the subbasal ones inconspicuously coloured. 2nd and later instar caterpillars are darker (Figs. 9, 12, 13), showing the same basic colour pattern as older instars of other miletine caterpillars living in homopteran aggregations (compare MASCHWITZ *et al.*, 1985a). *A. subviolaceus* larvae have two conspicuous dark patches subdorsally on the 4th and 5th abdominal segments that contrast strongly with the relatively bright colour of the posterior area; in last instar caterpillars this area is nearly white (Figs. 14, 15). This colouration improves camouflage within the homopteran aggregations.

The shape of the pupa (Fig. 16) is typical for lycaenids. The pupa is fixed with the large cremaster to a silken bolster on the plant stem and additionally with a weak girdle, head down. The only pupa observed was 9.5 mm long. After strong mechanical stimulation it showed short vibratory movements of high frequency, but low amplitudes, thereby most likely producing stridulatory sounds as is typical for lycaenid pupae. The colouration was similar to that of the larvae, with cryptic small patterns in brighter or darker variations of olive or greyish brown providing camouflage on the twigs. We did not observe adult butterflies at the sites.



Figs.9 – 16. *Allotinus subviolaceus*. 9. Membracid aggregation attended by workers of *Anoplolepis longipes* on *Uncaria*. The abdomen of the ant on the right is clearly blown up with honeydew. In the centre, a medium-sized larva of *A. subviolaceus*. 10. Egg of *A. subviolaceus* on last instar nymph of unidentified membracid species. 11. First instar caterpillar of *A. subviolaceus* on young *Uncaria* leaf, length of larva approx. 2 mm. 12. First and second instar larvae (lines are 5 mm in length). 13. Half-grown larva (ca. $L_{3/4}$) on *Uncaria* stem. 14, 15. Lateral and dorsal view of mature caterpillar of *A. subviolaceus*. 16. Pupa of *A. subviolaceus* on stem of *Uncaria* (lateral view). The weak girdle is visible at the ventral part of the wing sheath. (All photographs except the microphotographs taken in the field in W. Malaysia by U. MASCHWITZ and W. A. NÄSSIG. SEM photograph by M. RUPPEL.)

Discussion

1. Larval nutritive strategies

Most species of the Miletinae whose larval biology is known feed on aphids or coccids (review : COTTRELL, 1984). Thus, aphidophagy and coccidophagy are likely to be the plesiomorphic larval nutritive strategies in the Miletinae. The small genus *Logania* represents this basic pattern (MOULTON, 1912; cited after ELIOT, pers. comm.). The species-rich genera *Miletus* and *Allotinus* in South East Asia apparently developed novel feeding specializations derived from the basic miletine strategy, thus opening additional niches. The species observed by us exhibit three different nutritive strategies.

a) *Maintenance of a broad spectrum of homopteran prey; possible use ants as oviposition cues* ("ant-dependent food selection" ?) :

Miletus boisduvali MOORE (ROEPKE, 1919) and *M. biggsii* both prey on aphids and coccids, the latter apparently only on those living in associations with *Dolichoderus* species and perhaps using the ants as oviposition cue. Other *Miletus* species seem to feed on either aphids or coccids only (*M. chinensis* : KERSHAW, 1905; *M. symethus petronius* : ELIOT, 1980; *M. nymphis fictus* : BARLOW, pers. comm.), apparently without depending on the ants attending these homopterans.

M. biggsii preys on both coccids and aphids, the latter belonging to several families including the Hormaphididae which possess a soldier caste. The aphid soldiers were observed to be effective defenders of their colonies against *Miletus* larvae. The *Miletus biggsii* caterpillars seem to depend on a special, intermediate aphid aggregation size : too small an aphid colony might mean starving after eating the whole colony, too large might mean being killed by the soldiers. The strong correlation between homopteran prey species used and association of these aphids and coccids with *Dolichoderus* ants leads us to the conclusion that the ants are used by the females of *M. biggsii* as oviposition cues as described by ATSATT (1981) and PIERCE & ELGAR (1985) for phytophagous myrmecophilous lycaenids. *Dolichoderus* ants are very abundant in the area of our studies and thus many oviposition habitats for *M. biggsii* are available.

b) *Evolution of kleptoparasitism in ant nests starting from larval coccidophagy* :

Parasitic relationships between lycaenids and ants are not uncommon. One type is the "indirect parasitism" of lycaenid larvae on symbiotic associations of ants with either myrmecophytic plants (MASCHWITZ *et al.*, 1984) or trophobiotic homopterans. This is typical for the miletine larvae which destroy trophobiotic ant-homopteran associations by feeding on aphids or coccids. The more direct type of parasitism is represented by lycaenid larvae which live in the nests of ants without being attacked by them. These larvae (at least the final instars) feed on ant brood and/or sometimes even solicit regurgitation from the ants, thus parasitizing on the ant colony as a whole. This kind of relationship with ants is termed "kleptoparasitism" here. The

kleptoparasitic lycaenid species include the "phyto-predaceous" group of HENNING (1983a). The kleptoparasitism originated independently several times within the Lycaenidae, either starting from mutualistic myrmecophilous associations of Polyommata species with ants (e. g. *Maculinea* and *Lepidochrysops*, see CLARK & DICKSON, 1971; HENNING, 1983 a, 1983b; COTTRELL, 1984; THOMAS, 1984; WEIDEMANN, 1986) or from non-mutualistic myrmecoxenous relationships with ants as in the genera *Liphyra*, *Euliphyra*, and possibly *Thestor* (CLARK & DICKSON, 1971; COTTRELL, 1984). The kleptoparasitism involves complex adoption strategies of the lycaenids towards the ants, including release of brood-carrying behaviour, following ant's scent trails and others (HENNING, 1983a, 1983b; SCHROTH & MASCHWITZ, 1984; THOMAS 1984).

Allotinus apries offers an interesting example of the evolution of kleptoparasitism in the Miletinae. The L₁ is coccidophagous, the L₂ is carried into the carton nests by *Myrmicaria* ants. There the larva probably feeds on ant brood until pupation. The carrying behaviour is probably stimulated chemically and further enhanced by the lateral thoracic protuberances (an interesting parallelism to the "humping" behaviour of *Maculinea arion* just before the adoption by *Myrmica* ants, see CHAPMAN, 1915; THOMAS, 1977). The scarcity of *A. apries* (ELIOT, pers. comm.) may be explained by this highly specialized life history, making the lycaenid dependent on *Myrmicaria*-coccid associations first and *Myrmicaria* colonies later.

c) *Shift of the food range from Sternorrhyncha to Auchenorrhyncha:*

Auchenorrhynchophagy has evolved a few times independently within the Miletinae (e.g. the African genera *Megalopalpus*, *Lachnocnema* and *Thestor*, see LAMBORN, 1914; CLARK & DICKSON, 1971; COTTRELL, 1984). In South East Asia only two *Allotinus* species (including our own observations) are known to feed on membracids. Auchenorrhyncha seem to be a less adequate food source for Miletinae, probably because they do not normally form large aggregations; moreover, they are in general larger and more agile than Sternorrhyncha and therefore a less readily accessible food resource for small and slow L₁ caterpillars. Aggregations are only found in those Auchenorrhyncha that exhibit brood-caring behaviour or form trophobiotic associations with ants, as for instance membracids (WOOD, 1984).

Allotinus subviolaceus does not deviate from the predaceous life habits normally found within the Miletinae: its larvae feed on membracid nymphs as other Miletinae do with sternorrhynchans. But at least sometimes the eggs are laid directly on the membracids (see Fig. 10), thus providing an interesting preadaptation for larval ectoparasitism. Such egg deposition patterns have been reported for the African *Megalopalpus* as well (LAMBORN, 1914; review: COTTRELL, 1984). Thus the potential for the evolution of larval ectoparasitism is given in certain groups of the Miletinae. Recently KITCHING (1987) could indeed show that *Allotinus major* from Sulawesi lives as an ectoparasite on membracid nymphs in the younger larval instars.

There are evidently only two additional examples of true larval ectoparasitism (in early instars; older caterpillars may be predacious) on living insects within the large order Lepidoptera: The first one is the pyralid moth *Sthenauge* (*Sthenobaea* according

to FLETCHER & NYE, 1984) *parasiticus* JORDAN from Brazil, living on the back of large saturniid caterpillars of the genera *Automeris* and *Dirphia* and feeding on their scoli (JORDAN, 1926). The second example is the family Epipyropidae, where the known caterpillars feed on living homopterans (e. g., Flatidae; KRAMPL & DLABOLA, 1983), at first parasitic, then predacious.

Our observations indicate that the South East Asian Miletini show a greater variety of nutritive strategies than hitherto known. The variety exhibited seems to be of the same magnitude as the one found in the African miletine species. To overlook the whole spectrum and to complete our fragmentary knowledge further detailed studies are required.

2. Larval myrmecoxeny

The larvae of the Miletinae all lack a dorsal nectary organ (DNO) and tentacular organs (TOs), which are the larval organs responsible for myrmecophilous associations between ants and lycaenid caterpillars. Therefore they should be termed myrmecoxenous following KITCHING & LUKE (1985). Only the pore cupola organs (PCOs) are present in Miletinae larvae. The PCOs are supposed to suppress the ants' aggressiveness, and, indeed, the larvae of Miletinae were largely ignored by the ants attending the trophobiotic homopterans. Neither aggressiveness nor intensive palpation occurred. Thus, the miletine larvae exhibit typical myrmecoxenous characteristics like, e. g., the Lycaeninae. Whether the epidermal organs recently discovered by KITCHING (1987) have any function in the ant-larva interactions remains to be investigated. Another problem to be solved is whether the miletine larvae benefit from the presence of ants in the trophobiotic homopteran associations as has been shown for phytophagous myrmecophilous lycaenids (PIERCE & MEAD, 1981; PIERCE & EAST-SEAL, 1986).

The above generalizations do not apply to the kleptoparasitic larvae. In the case of *Allotinus apries* a cue stimulating the ants to carry the larvae into the nest must exist. This signal (probably a chemical one, combined with the morphological specialization) needs to be detected. In any case, the kleptoparasitic larvae show a level of myrmecophily remarkably different from the myrmecoxeny of other Miletinae.

3. Imaginal myrmecophily

In contrast to most of their larvae, at least some imagines of the Miletinae, e. g. *Miletus biggsii* and especially *Logania malayica*, have to be termed myrmecophilous. They apparently use ants as cues for adequate oviposition sites and possibly also as signals for feeding or resting places or courtship grounds. Why the butterflies are not treated aggressively by the ants is completely unknown. Probably the imagines produce appeasement-substances just as the larvae do. As the ants generally defend their trophobiotic partners against enemies, it seems likely that the imagines of *Logania malayica*, which rest within the ant-attended aphid colonies during the night as well as during most of the day, use this place as a kind of "enemy-free shelter". As imaginal myrmecophily is rare in the Lycaenidae as it is in the Lepidoptera in general,

further studies should include this phenomenon as well.

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References

- AOKI, S., 1982. Soldiers and altruistic dispersal in aphids. In M. BREED, Ch. MICHENER & E. EVANS eds. *The biology of social insects. Proc. IX. Congr. IUSSI* (Boulder, Co.; Westview Press).
- 1987. Evolution of sterile soldiers in aphids. In Y. ITÔ, J.L. BROWN & I. KIKKAWA eds. *Animal societies: theories and facts*. Tokyo (Japan Sci. Soc. Press).
- ATSATT, P.R., 1981. Ant-dependent food plant selection by the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). *Oecologia* (Berlin), **48**: 60–63.
- CHAPMAN, T.A., 1915. Observations completing an outline of the life-history of *Lycaena arion* L. *Trans. Ent. Soc. London*, **1915**: 298–312, 3 pls.
- CLARK, G.C. & C.G.C. DICKSON, 1971. *Life histories of the South African lycaenid butterflies*. Cape Town (Purnell).
- CORBET, A.S. & H.M. PENDLEBURY, 1978. *The butterflies of the Malay Peninsula* (3rd ed., revised by J. N. ELIOT). Kuala Lumpur (Malayan Nature Soc.).
- COTTRELL, C.B., 1984. Aphytophagy in butterflies: its relationship to myrmecophily. *Zool. J. Linn. Soc.*, **79**: 1–57.
- ELIOT, J.N., 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bull. Brit. Mus. Nat. Hist. (Entomol.)*, **28**: 373–505.
- 1980. New information on the butterflies of the Malay Peninsula. *Malay. Nat. J.*, **33**: 137–155.
- 1986. A review of the Miletini (Lepidoptera: Lycaenidae). *Bull. Brit. Mus. Nat. Hist. (Entomol.)*, **53** (1): 1–105.
- FLETCHER, D.S. & I.W.B. NYE, 1984. *The generic names of moths of the world*, vol. 5. London (Trustees BMNH).
- HENNING, S.F., 1983a. Biological groups within the Lycaenidae (Lepidoptera). *J. ent. Soc. sth. Afr.*, **46**: 65–85.
- 1983b. Chemical communication between lycaenid larvae (Lepidoptera: Lycaenidae) and ants (Hymenoptera: Formicidae). *J. ent. Soc. sth. Afr.*, **46**: 341–366.
- JORDAN, K., 1926. On a pyralid parasitic as larva on spiny saturnian caterpillars at Pará. *Novit. Zool.*, **33**: 367–370.
- KERSHAW, J.C.W., 1905. The life history of *Gerydus chinensis*, FELDER. *Trans. Ent. Soc. London*, **1905**: 1–4, 1 pl.
- KITCHING, R.L., 1987. Aspects of the natural history of the lycaenid butterfly *Allotinus major* in Sulawesi. *J. Nat. Hist.*, **21**: 535–544.
- , & B. LUKE, 1985. The myrmecophilous organs of the larvae of some British Lycaenidae (Lepidoptera): a comparative study. *J. Nat. Hist.*, **19**: 259–276.

- KRAMPL, F. & J. DLABOLA, 1983. A new genus and species of Epipyropid moth from Iran ectoparasitic on a new *Mesophantia* species, with a revision of the host genus (Lepidoptera, Epipyropidae; Homoptera, Flatidae). *Acta ent. bohemoslov.*, **80**: 451–472.
- LAMBORN, W.A., 1914. On the relationship between certain West African insects, especially ants, Lycaenidae and Homoptera. *Trans. Ent. Soc. London*, **1913**: 436–498, 1 pl.
- MASCHWITZ, U., DUMPERT, K. & P. SEBASTIAN, 1985a. Morphological and behavioural adaptations of homopterophagous blues (Lepidoptera: Lycaenidae). *Entomol. Gener.*, **11**: 85–90.
- , SCHROTH, M., HÄNEL, H. & Y.P. THO, 1984. Lycaenids parasitizing symbiotic plant-ant partnerships. *Oecologia* (Berlin), **64**: 78–80.
- , ———, ———, & ——— 1985b. Aspects of the larval biology of myrmecophilous lycaenids from West Malaysia (Lepidoptera). *Nachr. ent. Ver. Apollo*, Frankfurt, N.F., **6**: 181–200.
- MOULTON, J.C., 1912. A list of the butterflies of Borneo with descriptions of new species. *J. Straits Branch R. Asiatic Soc.*, **6**: 73 ff., here p.77.
- PIERCE, N.E. & S. EASTSEAL, 1986. The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. *J. Anim. Ecol.*, **55**: 451–462.
- , & M.A. ELGAR, 1985. The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. *Behav. Ecol. Sociobiol.*, **16**: 209–222.
- , & P.S. MEAD, 1981. Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. *Science*, **112**: 1185–1187.
- ROEPKE, W., 1919. Zur Myrmecophilie von *Gerydus boisduvali* MOORE (Lep. Rhop. Lycaenid.) *Tijdschr. Entomol.*, **61**: 1–16, 3 pls.
- SCHROTH, M. & U. MASCHWITZ, 1984. Zur Larvalbiologie und Wirtsfindung von *Maculinea teleius* (Lepidoptera: Lycaenidae), eines Parasiten von *Myrmica laevinodis* (Hymenoptera: Formicidae). *Entomol. Gener.*, **9**: 225–230.
- THOMAS, J.A., 1977. The ecology of the large blue butterfly. *Rep. Inst. Terr. Ecol.*, **1976**: 25–27.
- 1984. The behaviour and habitat requirements of *Maculinea nausithous* (the dusky large blue butterfly) and *M. teleius* (the scarce large blue) in France. *Biolog. Conservat.*, **28**: 325–347.
- WEIDEMANN, H.-J., 1986. *Tagfalter, Band 1, Entwicklung — Lebensweise*. Melsungen (J. Neumann-Neudamm).
- WOOD, T.K., 1984. Life history patterns of tropical membracids (Homoptera: Membracidae). *Sociobiology*, **8**: 299–344.

摘 要

マレー半島におけるアシナガシジミ亜科の幼虫の肉食性と客棲性および成虫の好蟻性
(Ulrich MASCHWITZ, Wolfgang A. NÄSSIG, Klaus DUMPERT & Konrad FIEDLER)

アシナガシジミ亜科の幼虫はすべて肉食であり、同翅亜目の昆虫およびその分泌物を食物としている。東南アジアの *Logania*, *Miletus*, *Allotinus* の3属の食性についてはほとんど知られていなかったが、我々の最近の研究で、これらの幼虫が肉食性であることが確認された。またアリの巣中での盗食寄生など、今まで知られなかった食性についての知見を得たので報告する。観察および実験は1986年から1987年にかけてクアラルンプールのMalaya大学Ulu Gombak野外研究センターとその付近で行われた。

結果

Logania malayica malayica DISTANT, 1884

成虫は森林中の開けた場所にみられ、ショウガ科の *Achasma* 属に寄生した *Pseudoregma* 属のアブラムシのコロニーで分泌物を摂食していた。夜間にはコロニー中で休む個体が観察された。アブラムシは *Lepto-*

*thorax*属のアリに世話をされていた。*Pseudoregma*属のアブラムシは兵隊アブラムシを持ち、大コロニーではその数は多い。チョウの卵は小コロニーでのみ発見され、また発見できた幼虫は1頭のみであった。兵隊アブラムシの反応をみるため、他から採集した*Miletus*属の種々のサイズの幼虫をアブラムシのコロニー中に入れたところ幼虫はすぐに攻撃され、若齢幼虫は殺されることもあった。

Miletus biggsii (DISTANT, 1884)

1984年、カイガラムシのコロニーの中に産卵する雌を観察したのに続いてショウガ科の植物に寄生した*Pseudoregma*属のアブラムシの分泌物を摂食していた雌を観察した。いずれの場合もカイガラムシやアブラムシは*Dolichoderus* (カタアリ)属のアリに世話をされていた。このアリの存在が雌にとって産卵場所の目印になっていると思われる。チョウの卵は大コロニーでも発見したが、幼虫は兵隊アブラムシがいないか、少ない小コロニーでのみ見られた。幼虫はアブラムシを摂食していた。

Allotinus (Paragerydus) substrigosus substrigosus (MOORE, 1884)

ショウガ科の*Achasma*属に寄生した*Pseudoregma*属のコロニー中に数日滞在し、アブラムシの分泌物を摂食する1頭の雄を観察した。アブラムシは*Crematogaster* (シリアゲアリ)属のアリに世話をされていた。兵隊アブラムシが少ないコロニー中に卵と幼虫を発見した。

A. (P.) apries FRUHSTORFER, 1913

雌はフタフシアリ亜科の*Myrmicaria lutea*の働きアリに世話をされたカイガラムシの集団中に産卵する。1齢幼虫はカイガラムシを摂食する。2齢幼虫は*M. lutea*の働きアリによりアリの巣の中に運ばれ、アリの幼虫を摂食して成長する。蛹化は巣中で行われ、成虫は羽化後脱出する。

A. (Allotinus) subviolaceus C. & R. FELDER (1865)

幼虫はアカネ科の*Uncaria* sp. 上の種名の判明しないツノゼミ(頸吻群)が集まっている場所でみられた。ここにはヤマアリ亜科に属する*Anoplolepis longipes* (アシナガキアリ)が訪れていた。産卵は同翅類の中か、近くの茎にされるが、3度若虫に産卵されたのを観察した。幼虫はツノゼミの若齢幼虫を食べる。蛹は植物の茎上に見られた。

考察

1. 幼虫の栄養戦略

腹吻群(アブラムシ、カイガラムシ)食は*Miletinae*幼虫の祖先形質の栄養戦略であり、*Logania*は基本パターンを示す。多くの種を含む*Miletus*と*Allotinus*はより特化した食性を発展させている。我々の観察した種には3種の栄養戦略がみられた。

a) 広範囲の同翅類食の維持と産卵目印としてのアリ利用の可能性

*Miletus boisduvali*と*M. biggsii*はアブラムシとカイガラムシを食べる。*M. biggsii*は兵隊を持つ種も含め数科にわたるアブラムシを摂食する一方、兵隊アブラムシは幼虫に対しコロニー防衛をする。幼虫は中規模のサイズのコロニーに依存しているようである。コロニーのサイズが小さすぎると食物が少なく、大きすぎると兵隊アブラムシに殺されるからである。アブラムシは*Dolichoderus*属のアリと結び付いているが、このアリの存在が雌にとって産卵の目印となっていると思われる。

b) カイガラムシ食からアリの巣中での盗食寄生への進化

シジミチョウとアリの寄生関係には2タイプある。一つはアリと好蟻性植物や栄養共生同翅類との共生関係に依存するシジミの間接的寄生というべきものであり、*Miletinae*の幼虫は典型的である。より直接的なタイプはアリの巣中で攻撃を受けることなく生活するタイプである。幼虫(少なくとも終齢)はアリの幼生を食べたり、アリからの給餌、またはその両方で生育し、全くアリのコロニーに寄生している。アリとのこのような関係をここでは盗食寄生と呼ぶ。盗食寄生は数回にわたり独立的に生じたと考えられる。すなわちアリとPolyommatainae(ヒメシジミ亜科)の幼虫の共生的好蟻性関係からスタートしたもの(*Maculinea*(ゴマシジミ属)や*Lepidochrysops*)と、*Liphyra*(アリノスシジミ属)、*Euliphyra*、そしてたぶん*Thestor*属に

おけるアリとの非共生的客棲性から出発したものが考えられる。*A. apries* においてはアリによる幼虫運搬行動はたぶん化学的に刺激され、更にlateral thoracic protuberancesによって高められると思われる。

c) 腹吻群から頸吻群への食物の移行

頸吻群食はMiletinaeの中に少ない機会ながら独立的に進化してきた。東南アジアでは2種の*Allotinus*のみがツノゼミ食として知られる。頸吻群はMiletinaeにとって食物として十分とはいえないように思える。なぜなら通常大きな集団は作らないし、腹吻群に比べ大きく敏活であり、1齢幼虫にとっては受け入れにくい食物であるためである。*A. subviolaceus* はツノゼミの若虫を食い、また卵が直接ツノゼミに産まれることもあり、幼虫の外部寄生の興味ある前適応を示してくれる。このような産卵パターンはアフリカの*Megalopalpus*でもみられる。最近セレベスの*A. major* で若齢期にはツノゼミの若虫上で外部寄生として生活していることが報告された。

東南アジアのMiletiniは以前知られていたより変化に富んだ栄養戦略をとっている。しかしその全貌を明らかにするには更に研究が必要である。

2. 幼虫の客棲性

Miletinaeの幼虫はアリとシジミチョウ幼虫の好蟻棲関係を信頼されるものにする器官である背部蜜腺とtentacular器官を欠く。それゆえKITCHING & LUKE (1985) によると客棲性と言われる。Miletinaeにはpore cupola器官のみが存在し、この器官はアリの攻撃性を抑えると考えられる。KITCHING (1987) によって発見された表皮器官がアリ—幼虫関係になんらかの機能を持つかどうか、Miletinaeの幼虫が植食性の好蟻性シジミチョウに見られるようなアリの存在によって利益を得ているかどうかは今後の研究の課題である。

A. apries にみられる盗食寄生は他のMiletinaeの客棲性とは明らか異なる好蟻性の一段階を示している。

3. 成虫の好蟻性

Miletus biggsii と *Logania malayica* の成虫は好蟻性を示す。彼らは明らかにアリを産卵場所の目印にしているし、また採餌や休息、交尾の場所の目印としても利用している可能性がある。なぜチョウがアリによって攻撃的な扱いを受けないかは不明であるが、おそらく幼虫同様なだめ物質を生産しているのであろう。アリは一般的に栄養共生パートナーを天敵から守るので、*L. malayica* の成虫が昼ばかりでなく夜もアリに世話をされたアブラムシのコロニー内で過ごすことは、チョウにとって天敵無しの場所を利用していることにもなる。成虫の好蟻性についてはシジミチョウ科では希であり更に研究が必要であらう。(文責 伴野英雄)